

FOSSIL VERTEBRATES (MAMMALIA AND REPTILIA) FROM CAPO MANNU FORMATION (LATE PLIOCENE, SARDINIA, ITALY), WITH DESCRIPTION OF A NEW *TESTUDO* (CHELONII, TESTUDINIDAE) SPECIES

LAURA ABBAZZI¹, SALVATORE CARBONI², MASSIMO DELFINO¹, GIANNI GALLAI¹,
LUCIANO LECCA² & LORENZO ROOK^{1*}

Received: May 10, 2007; accepted: October 16, 2007

Key words: Stratigraphy, Vertebrate fauna, *Testudo*, Pliocene, Mandriola, Capo Mannu, Sardinia.

Abstract. In the North-West Sinis Peninsula (Western Sardinia) a stratigraphic sequence, the Capo Mannu Fm., that evolves from marine-littoral to continental-dunar, is present. A vertebrate fauna is reported within the middle part of this coastal dune complex. These new remains, here referred to as the Capo Mannu D4 Local Fauna, are slightly younger in the sedimentary succession than the Local Fauna known in the literature as Mandriola and here re-named the Capo Mannu D1 Local Fauna.

Vertebrates from Capo Mannu D4 include reptiles (Chelonii) and mammals (Bovidae and Suidae). The tortoise fossil shows peculiarities of shape that require the naming of a new species. The suid material includes a fragmentary palate and a partial mandible, referable to the endemic species *Sus sondaari*. Bovids are well represented in the assemblage, although quite fragmentary. They have been identified as belonging to at least two forms. One of these is comparable in morphology to *Nesogoral*, one of the most characteristic taxa of the Late Pliocene-Early Pleistocene Sardinian endemic fauna (the so called “*Nesogoral* complex”). On the whole, the Capo Mannu D4 assemblages open a new window on the Plio-Pleistocene terrestrial faunas of the Sardinian Island.

Riassunto. Nella penisola del Sinis (Sardegna Occidentale) affiora la formazione Pliocenica di Capo Mannu, che è caratterizzata da un’alternanza di corpi dunari e paleosuoli ed evidenzia un’evoluzione paleoambientale da marino-litorale a continentale. Nella parte intermedia di questo complesso dunare sono stati rinvenuti resti fossili di vertebrati di ambiente terrestre. Questi resti vengono attribuiti, nel presente lavoro, alla “Fauna locale Capo Mannu D4”, in riferimento all’unità dunare in cui sono stati rinvenuti. Da un livello, stratigraficamente al di sotto della fauna Capo Mannu D4, provengono i fossili riferiti in

letteratura alla “fauna di Mandriola”, che viene qui rinominata “Fauna locale Capo Mannu D1”.

I vertebrati della fauna Capo Mannu D4 appartengono a rettili (Ordine Chelonii) e mammiferi (Ordine Artiodactyla, famiglie Bovidae e Suidae). Il fossile di testuggine mostra caratteri che consentono la definizione di una nuova specie. Il suide è rappresentato da reperti che indicano la sua appartenenza alla specie endemica *Sus sondaari*. I bovidi sono il gruppo meglio rappresentato, benché i resti siano piuttosto frammentari. Essi appartengono almeno a due forme distinte. Una di queste è confrontabile al genere *Nesogoral*, che rappresenta uno degli elementi più caratteristici della fauna endemica sarda attribuita al cosiddetto complesso a “*Nesogoral*”, che documenta un intervallo di tempo dal Pliocene superiore alla parte iniziale del Pleistocene inferiore. L’associazione di Capo Mannu D4 rappresenta quindi una delle più antiche segnalazioni della presenza del complesso a *Nesogoral* nell’ambiente insulare Sardo.

Introduction

A small vertebrate fauna was found within an interdune deposit at the base of the Capo Mannu Formation, overlying the Mandriola Limestone (North-West Sinis, Fig. 1). These remains were first reported by Pecorini et al. (1974) as Middle Pliocene in age.

Other vertebrate remains found in the dune complex of the Capo Mannu Formation have been recovered by two of us (SC and LL). These new remains were included in a new stratigraphic reconstruction of the Mandriola-Capo Mannu succession in a previous paper (Carboni & Lecca 1995).

1 * Corresponding author. Dipartimento di Scienze della Terra, Università degli Studi di Firenze - Via G. La Pira 4, 50121 Firenze. E-mail: laura.abbazzi@unifi.it; massimo.delfino@unifi.it; gianni.gallai@unifi.it; lorenzo.rook@unifi.it.

2 Dipartimento di Scienze della Terra, Università degli Studi di Cagliari - Via Trentino 51, 09127 Cagliari. E-mail: carbonis@unica.it; leccal@unica.it.

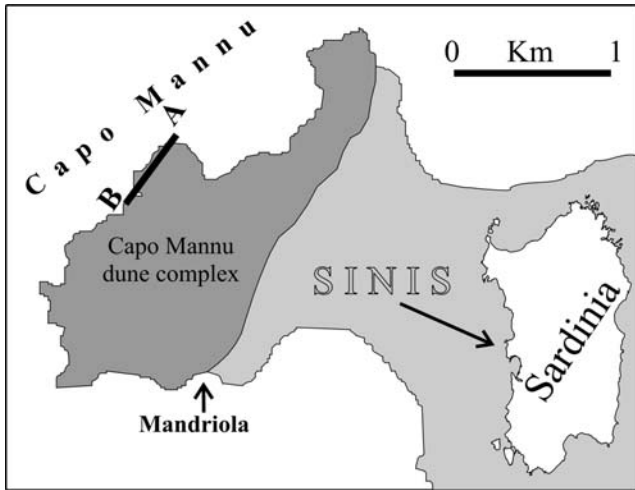


Fig. 1 - Location of Capo Mannu and Mandriola sections. A-B: location of the cross-section shown in Fig. 3.

The aim of this paper is to describe in detail the unpublished vertebrate remains of the Capo Mannu Fm., as well as to provide a detailed stratigraphic context for this dune complex and the vertebrates occurring therein.

Stratigraphy

The Pliocene-Pleistocene sequence in the northern Sinis (Mandriola Limestone and Capo Mannu Fm.) overlies (with a possible erosional unconformity) a Middle Miocene-Messinian sequence resting on the Oligo-Miocene volcanic basement (Fig. 2). The Pliocene-Pleistocene sequence can be summarized as a shoreface unit followed by various dune units, locally overlain by

Upper Pleistocene beach sandstones and conglomerates referred to the Tyrrhenian transgression (Marine Isotopic Stage, MIS 5e) and continental talus referred to the Marine Isotopic Stages MIS 4-2 (Carboni & Lecca 1985, 1995; Lecca & Carboni 2007).

Mandriola Limestone

The Mandriola Limestone outcrops at the edge of the North-West Sinis area. It has been referred to the Lower Messinian as “Calcarei Laminati del Sinis” by Cherchi et al. (1978). Seismostratigraphic studies on Pliocene hemipelagic marl sampled on the continental shelf (Lecca et al. 1986), suggest that the Mandriola Limestone is stratigraphically situated a few tens of metres above the Pliocene hemipelagic marl. Biostratigraphic studies recognized that this marl belongs to the *Discoaster tamalis* Zone, *Reticulofenestra pseudoumbilica* Subzone, NN 15 (approximately 3.5 Ma; Francolini et al. 1990). The Mandriola Limestone is mainly constituted by a foraminiferal grainstone with large ripple cross-laminations and hummocky structures of shoreface environment. This unit, about 10 m thick, gently dips westward and outcrops for approximately 1.5 km. The upper part contains several storm-related levels that are very rich in pelecypods. Within these levels are interbedded terrigenous sediments containing sparse rounded clasts of Messinian limestones (“Calcarei Laminati del Sinis”) and alkaline basalts. The origin of the volcanic clasts may be individuated in the Montiferru and Sinis areas, where the radiometric ages of related volcanites are 3.9 Ma (“lower basanites” of the Montiferru volcanic complex), 3.12 Ma (basalts of San Salvatore di Sinis) and 2.8-3.0 Ma (basalts of the southern side of the Montiferru volcanic complex; Beccaluva et

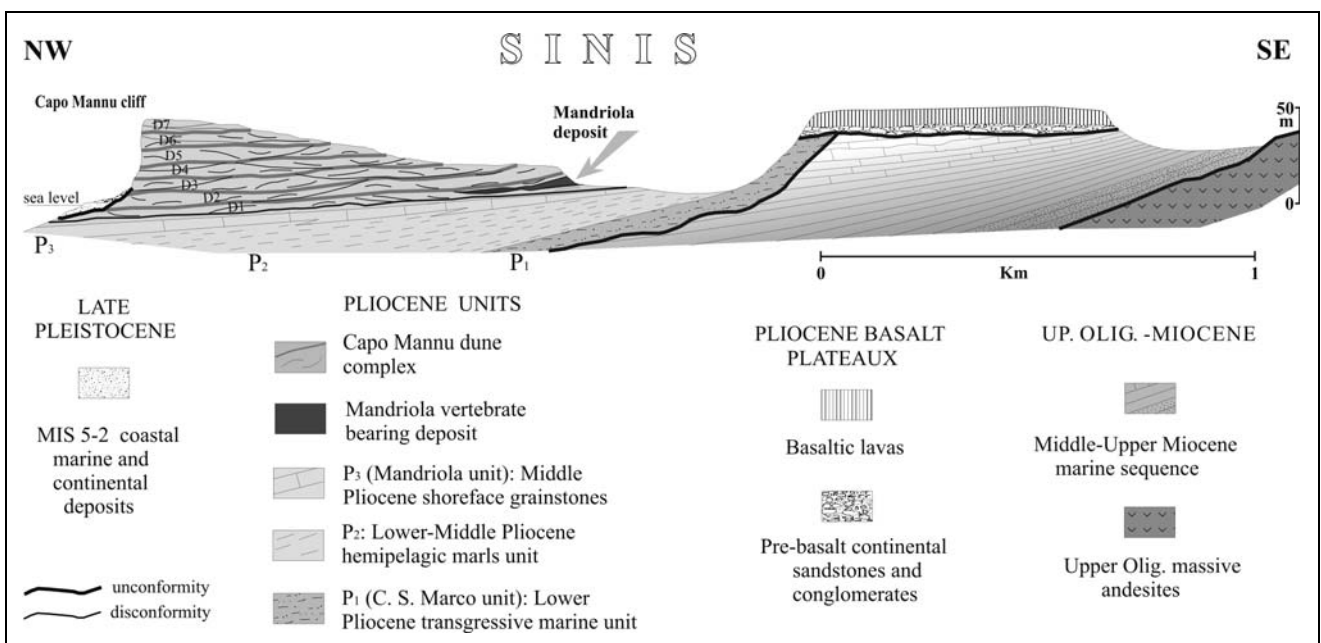


Fig. 2 - Synthetic cross-section of the Sinis (Capo San Marco - Capo Mannu) stratigraphic units and location of faunal deposits.

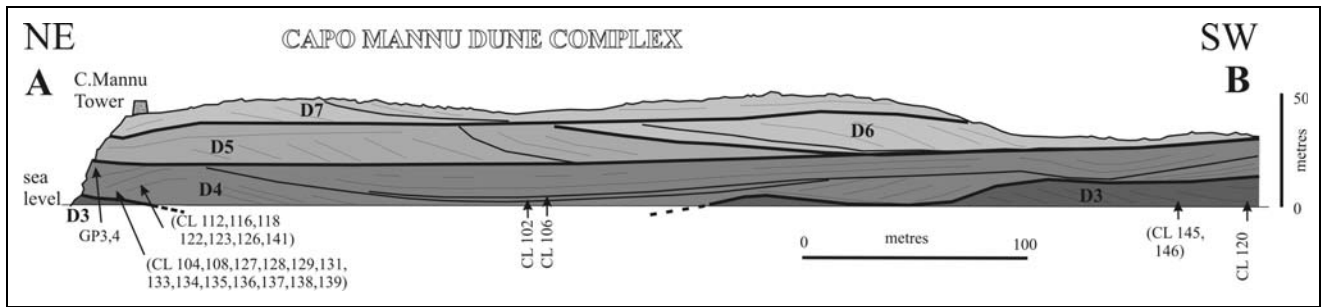


Fig. 3 - Capo Mannu dune complex upper part cross-section and detailed location of collected fossil remains.

al. 1985). On the basis of the full data set the above-mentioned sedimentary shoreface sequence is to be interpreted at the Zanclean-Piacenzian transition (Carboni & Lecca 1995).

The dune complex of the Capo Mannu Formation

The Capo Mannu Formation (CMF), primarily defined by Pecorini et al. (1974), is a calcareous and terrigenous 50 m thick sand body, made up of four stacked and laterally continuous dune units, overlain by three other dune units of lesser lateral continuity. On the whole, at least nineteen dune subunits can be identified in the aeolian complex (Carboni & Lecca 1995; Fig. 2).

The hierarchy of the depositional discontinuities shows internal boundaries of 3rd, 2nd, and 1st order *sensu* Brookfield (1977). The 1st order boundaries, generally represented by reddish clayey-silty sediments, may be associated both with interdune deposits and with interruptions of the eolian processes caused by climate change.

The first dune unit (D1), at the base of the CMF, consists of slightly dipping foraminiferal aeolian banks with at least two interbedded dump or clayey pond deposits at the base of the lee side of the dune. The Capo Mannu D1 local fauna (also known in the literature as Mandriola; see below) derives from the first clayey deposit (Fig. 2). This unit extends throughout the coastline between Mandriola and the Capo Mannu promontory, with a total thickness of approximately 3-4 m.

The next three overlying dune units (D2, D3 and D4) are developed along the entire Capo Mannu cliff. They exhibit distinct structuring which often differs markedly in grain size, composition, textural features and degree of diagenesis, and they display numerous discontinuities of lower order in the accretion architecture, in places with abundant root traces. The composition of such units varies both laterally and vertically, shifting from levels with high content of brackish benthic foraminifers (*Cibicides*, *Elphidium*, Rotalinidae, Miliolidae) and Ostracoda to levels with a dominant terrigenous siliciclastic component. In some units, a bioclastic component of pelecypods is dominant, form-

ing 10 cm thick beds, mainly consisting of up to 0.5 cm fragments of pelecypods alternated with level of similar thickness consisting of finer bioclastic sediments. Such units display a significant lateral continuity and an important aggradational component, and thus form tabular accretions which are on average 10-12 m thick.

In the dune subunit characterized by the finer bioclastic facies, the main depositional structures are represented by discontinuous compound sets of cyclic crossbeds and reactivation surfaces of low angle. The accretion is highlighted by prograding parallel laminar sets tending to sigmoidal shapes. These structures develop laterally by moderate fluctuations in the flow direction, ranging from south-eastward to north-eastward, producing some herringbone structures.

The bioclast-rich pelecypod subunit displays an oblique parallel tabular set 3-4 m thick developed roughly south-eastward at angles of up to 30°. It must be noted that in the interdune levels and within the massive strata of the D3 and D4 dune units, an exemplar of the tortoise (Tegas 2000) and some of the vertebrate remains (described below) have been found (Figs. 2, 3).

The last three dune units (D5, D6 and D7), in the upper part of the dune complex, are laterally discontinuous and also composed of calcareous sandstones with foraminifers with variable terrigenous contents. Their internal geometry is more varied and usually shows tabular and low-angle sigmoidal prograding coset, low planar parallel in the higher parts. In these units the components are lithic-quartzose and bio-detrital (benthic microfauna).

The 1st order boundaries with reddish clayey-silty sediments separate the main seven units, and minor unconformities indicate several dune subunits within each main unit. These reddish sediments show a quartzose terrigenous component with homogenous fine sand-silt grain-size. The clay percentage varies from entirely clayey laminae to calcareous and iron/manganese films. The reddish sediment layers are up to 2 m thick, but they tend to thin laterally. Generally, the higher part contains abundant root traces, which may contain vertebrate bones and shells of Gastropoda Pulmonata. The very sandy sediments of the first-order unconformities

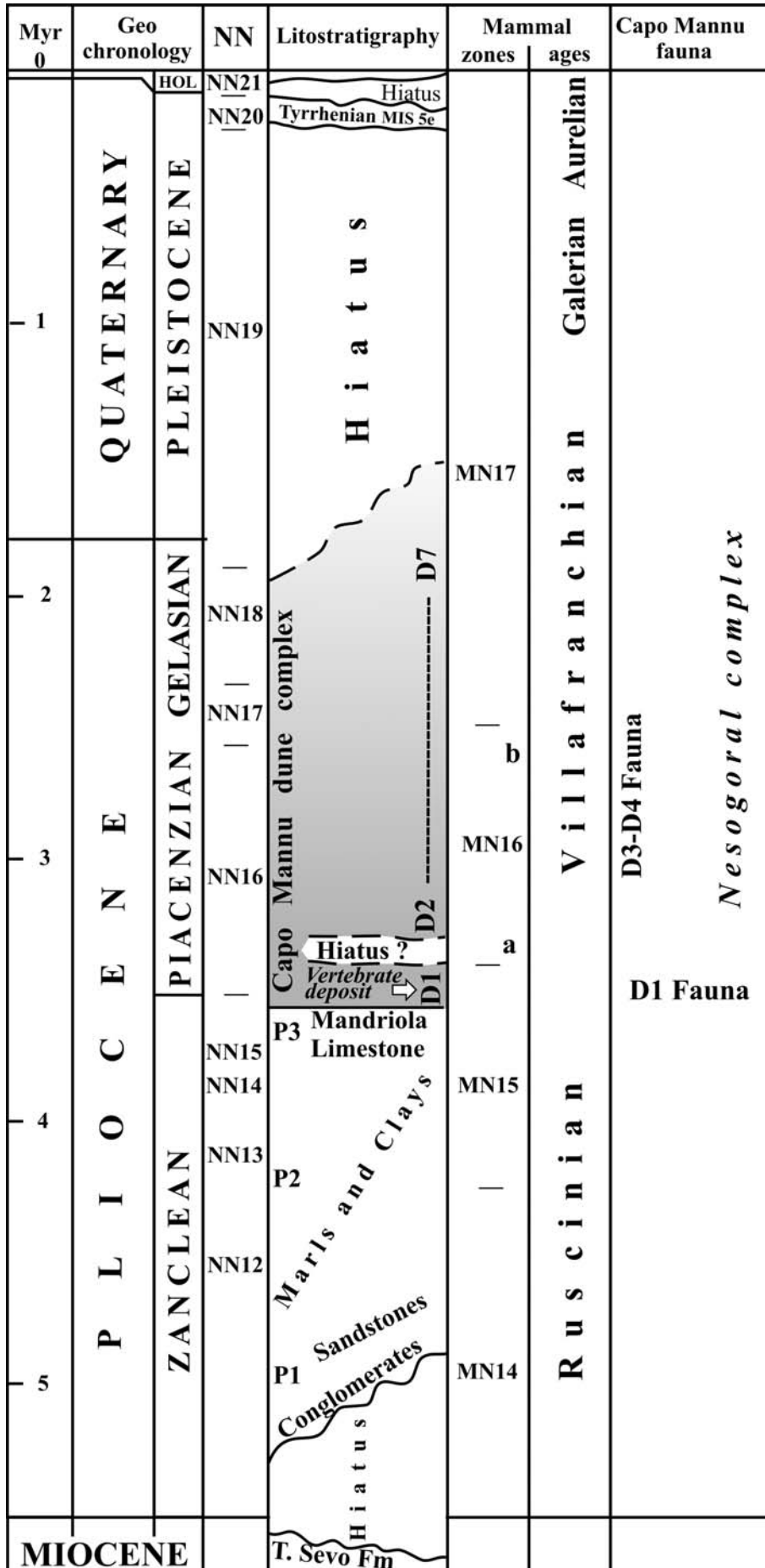


Fig. 4 - Chronological scheme and correlation of Capo Mannu local faunas with the bio-chronological mammal units.

must be attributed to re-sedimentation of finer grains derived from large dunes of a low energy aeolian regime in a wet climate.

Fossil vertebrates from the Capo Mannu Formation

Capo Mannu D1 local fauna: a debated chronological attribution

The occurrence of a small vertebrate assemblage in the interdune damp or pond deposits at the base of the Capo Mannu Fm. (Fig. 2, "Mandriola deposit") was originally reported by Pecorini et al. (1974). These authors attributed the vertebrate assemblage to the Middle Pliocene on the basis of biochronologic interpretations.

This small assemblage has been reported in the literature with different names. While most authors use the hamlet name "Mandriola", others (e.g. van der Made 1988, 1999) refer to it as "Capo Mannu". In order to avoid confusion with the name of the Lower to Middle Pliocene Mandriola Limestone, we propose here to name all the vertebrate fauna from the dune complex of the Capo Mannu Formation as Capo Mannu. Thus, the Mandriola mammal assemblage of previous authors will be referred to as the Capo Mannu D1 Local Fauna.

Some authors (Esu & Kotsakis 1979, 1983; Kotsakis 1980; Esu 1984), mainly on the basis of regional correlations, assigned the Capo Mannu D1 local fauna to MN 14 mammal unit of the early Ruscinian (Early Pliocene; Fig. 4), while others (e.g. van der Made 1988) agreed with the original (Pecorini et al. 1974) attribution to the Middle Pliocene.

The above mentioned biostratigraphic characterization of the Pliocene Mandriola Limestone (Francolini et al. 1990), constrains the age of the Capo Mannu D1 local fauna as corresponding to the time interval identified by marine biostratigraphy as the NN15/NN16 Zones (Fig. 4), in contrast with its attribution to the early Ruscinian (MN14; Kotsakis 1980; Esu & Kotsakis 1983; Esu 1984).

Recently, Angelone & Kotsakis (2001), on the basis of a new study of the Capo Mannu D1 murid (*Raghapodemus azzaroli*), assigned this fauna to the late Ruscinian. Therefore, they also correlate the age of this deposit with the Zanclean-Piacenzian transition, confirming the reconstruction of Carboni & Lecca (1995).

The vertebrate remains of the Capo Mannu D4 Local Fauna

Geological/sedimentological surveys of the Capo Mannu dune complex have recovered a number of vertebrate remains, in early times by Prof. G. Pecorini, and later by two of us (SC and LL), from a fossiliferous level corresponding to the base of the D4 dune (Fig. 3).

Some of the early remains were sent by G. Pecorini to P.L. Ambrosetti (Perugia) for taxonomic and biochronologic study, but they were never studied in detail. Thanks to the kind help of S. Gentili (Perugia), these remains (including a fragmentary skull and mandible of a small suid from D4, and a mandible and a few isolated teeth of a bovid from D1) have been re-located and made available for the present study, along with the entire collection of the Capo Mannu D4 fauna.

The fossils here described are housed in the Earth Sciences Department of Cagliari University. The acronym "GP" refers to the early collection by G. Pecorini, while the acronym "CL" refers to the recent collections.

Systematic Paleontology

Reptilia

Chelonii Brongniart, 1800

Testudinidae Batsch, 1788

Testudo Linnaeus, 1758

Testudo pecorinii Delfino n. sp.

Holotype: CL 102, a nearly complete shell housed in the Earth Science Department of Cagliari University, Italy (Figs. 5,6).

Etymology: the species is dedicated to Prof. G. Pecorini, honouring his outstanding contribution to the study of Sardinian geology.

Type locality: Capo Mannu (San Vero Milis Municipality); base of D4 dune of the Capo Mannu Formation; Upper Pliocene.

Diagnosis: the only fossil or extant member of the genus *Testudo*, group *Testudo* sensu stricto (therefore with a hinge between hypoplastra and xiphoplastra), characterized by five evident bosses sagittally aligned on the carapace; the bosses, developed in correspondence to the central region of the five vertebral scutes, are medio-laterally elongated, apically convex and well separated from each other.

Description

General preservation, shape and size. The shell is filled with matrix and is rather complete in terms of preserved skeletal elements, but even if it retains the overall morphology, the bone surface displays only few anatomical details. The original surface morphology, with furrows corresponding to the limits between the horny scutes, is preserved only in the antero-median region of the carapace and in a small antero-lateral corner of the plastron. A large portion of the bones (whitish in colour) has lost the outer layers and shows the eroded spongy inner tissue or is covered by a thin brownish arenaceous matrix.

The best-preserved area of the carapace is the medial part, since the anterior region is eroded to some extent and the posterior area is heavily damaged and incomplete (the posterior peripherals are only partly preserved). The plastron is nearly complete. A small

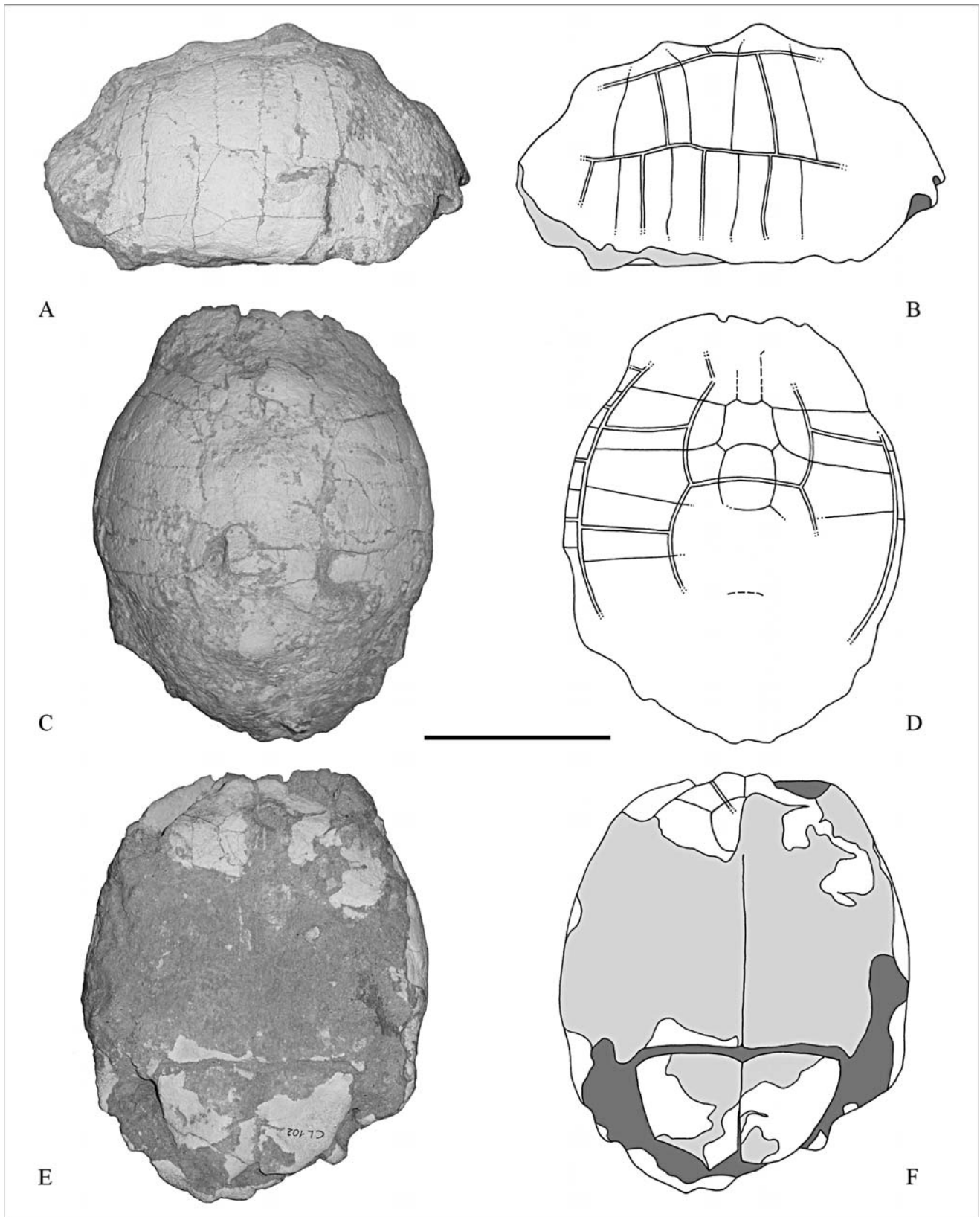


Fig. 5 - *Testudo pecorinii* Delfino n. sp. - Photographs and interpretative drawings of the shell in left lateral, upper and lower view. Dark grey indicates the matrix filling the shell, light grey indicates the thin concretion. The sutures involving neural elements have not been represented in lateral view. Scale: 10 cm.

portion of the surface of the fourth neural and the fourth right pleural is collapsed inward.

A possible bony structure of unknown origin (not necessarily belonging to the tortoise) is sealed by the matrix on the carapace in the region of the posterior-most right pleural.

As for the general shell shape, it is remarkable that, in dorsal view, the central region of the carapace (whose peripherals are engaged in the bridge) is rather rounded and separated from the anteriormost area (whose peripherals are free) by a slight constriction that is particularly evident on the left side; the development of the anterior area, and therefore the origin of such a constriction, is not known, since the peripherals are distally eroded or broken (mainly on the right side). A hint of a posterior constriction, corresponding to the boundary between the peripherals engaged in the bridge and those constituting the rim of the posterior shell opening, seems to be present, but the development of the posterior area of the shell cannot be evaluated because of the poor preservation.

Even if a weak dorso-ventral deformation cannot be ruled out, the anterior opening of the shell is rather narrow. The moderate concavity of the plastron could be related to such a possible weak deformation or represent a male character.

The shell has a total length of 22.5 cm, a maximum width of 17.8 cm and a maximum height of 12.2 cm.

Carapace. The first neural is barely visible but seems to be distinctly elongated and approximately rectangular; it is followed by an octagonal element and then by a rectangular one (whose antero-posterior length is greater than its width). The neurals are markedly convex and concave: such a morphology confers to the shell dorsal outline a “peaks and valleys” pattern, with peaks approximately corresponding to sutures between adjacent bony neurals (and the centre of the horny vertebral shields) and valleys to the neural surface (and therefore the furrows representing boundaries between adjacent shields); the protuberances have a uniformly convex apex (they are not apically flattened), do

not occupy the entire vertebral surface but only its central area (therefore protuberances are well separated from each other) and are medio-laterally elongated. On both sides, the first pleurals preserve only the posterior suture; the sutures delimiting the following two pleurals on the right and three on the left side are relatively visible: these trapezoidal elements show a typical alternation, with the widest base alternately placed dorsally and ventrally. Only the dorsal end of the pleurals participates in the protuberances generated by the neurals. The peripherals are better preserved on the left side, where at least five elements show clearly perceivable sutures, and they are rather large antero-posteriorly.

The horny mosaic is represented by the scute sulci of the second and third vertebrae (whose boundaries are not completely visible) and by the costals and marginals corresponding to the preserved bony plates. In dorsal view, the vertebral scutes are wider than the costal ones. In anterior and, to a lesser extent, posterior view, the area delimited by the vertebrae corresponds to a convexity of the shell outline delimited by a depression along the furrows between vertebrae and costals. In the proximal sector of each costal a hint of a boss is perceivable in some cases. Sutures between pleurals and peripherals correspond to the furrows between costals and marginals.

Plastron. The morphology of the plastron is much less interpretable than that of the carapace. Except for a short tract of the furrow between right gular and humeral, no furrows left by the horny shields are visible on the plastron. The epiplastra show a thick dorsal lip whose morphology cannot be evaluated in detail because of the presence of matrix filling the shell; the epiplastral area covered by the gular horny shields protrudes markedly anteriorly and represents a concavity of the ventral plastral surface. The entoplastron seems to be rather rounded. The gular shields penetrated into the entoplastron (but due to the presence of matrix it is not possible to assess how deeply they penetrated). The xiphiplastra are still joined together but they are distinctly separated from the hypoplastra by a gap of some millimetres: they have not been significantly dislocated

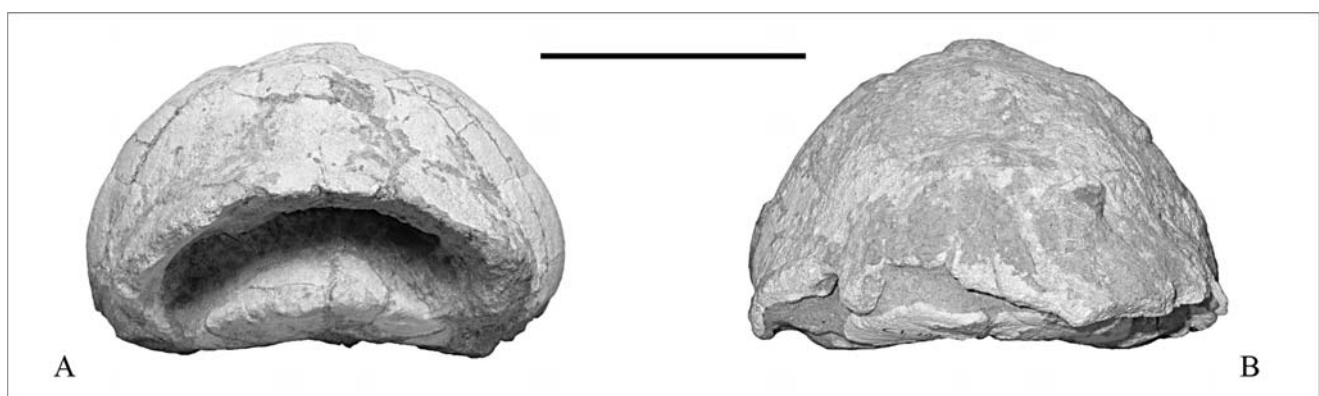


Fig. 6 - *Testudo pecorinii* Delfino n. sp. - Shell in anterior and posterior view. Scale: 10 cm.

thanks to the presence of the matrix. The boundaries between elements of the carapace and plastron not mentioned here are not visible.

Discussion. Due to the poor preservation, the morphology of all the bony plates and horny shields of the shell cannot be assessed. However, the morphology and relationships of the available elements, chiefly the shape alternation in the neurals and pleurals, as well as the correspondence of sutures between pleurals and peripherals to the furrows between costals and marginals, and the general architecture of the shell, are consistent with that of a member of the genus *Testudo*. The separation of the xiphiplastra from the hypoplastra indicates the presence of a hinge allowing movements of the posterior lobe of the plastron: such a characteristic identifies the *Testudo sensu stricto* group, represented by *T. graeca* and other extant forms inhabiting the Mediterranean region (see Lapparent de Broin 2000 for a list). The fact that the movable xiphiplastra were not dispersed prior to fossilization, suggests rapid burial of the shell before soft tissue decomposition. A further character shared with *T. graeca* (Amiranashvili 2000), and other species of its group, is the width of the vertebrals when compared to the costals.

The specimen from Capo Mannu is characterized by a peculiar morphology not known in any fossil or recent member of genus *Testudo s.s.*: the carapace surface is distinctly raised in correspondence with each of the vertebral scutes. Such a morphology is quite different from that sometimes occurring in wild *Testudo* populations (see Guyot Jackson 2004) or originating in captivity from an unbalanced diet, such as the calcium / phosphorous unbalanced ratio that causes a morphological anomaly known as “pyramiding” (in which, since the entire vertebral surface is convex, the bosses are contiguous and, moreover, usually apically flattened), but it is somehow reminiscent of the condition seen in some species of the genus *Psammobates* or “*Geochelone*”.

A weak development of dorsal protuberances is seen also in *Testudo amiatae* Pantanelli, 1892, from the Upper Miocene of southern Tuscany, but this species is characterized by xiphiplastra that are firmly sutured to hypoplastra and therefore cannot be ascribed to the *Testudo s.s.* group.

On the basis of this peculiar set of characters we propose a new species, *Testudo pecorinii*, belonging to the *Testudo s.s.* group.

The presence of a *Testudo s.s.* in the Late Pliocene of Capo Mannu represents the first fossil evidence for this group in peninsular and insular Italy. This group probably evolved in Europe since it can be traced back to the Turolian of Pikermi, Saloniki and Lesvos Island, but it is already present in the Late Pliocene of Morocco

and possibly in the Early Pliocene of Tunisia (see references in Lapparent de Broin 2000; 2001; 2002).

The Sardinian land tortoise fossil record is limited to a partial shell from the Plio-Pleistocene locality of Orosei (Abbazzi et al. 2004) referred to *T. cf. T. hermanni*, and to a few Holocene *Testudo* remains from archaeological contexts (cfr. Delfino 2002).

At present, three tortoises inhabit Sardinia, *T. hermanni*, *T. graeca* and *T. marginata*, but only the first one has been considered autochthonous (Amori et al. 1993; Lanza & Corti 1993). However, the presence of a morphologically peculiar *Testudo s.s.* in the Late Pliocene of Capo Mannu does not allow us to extrapolate a genetic continuity with the extant Sardinian populations belonging to this group, *T. graeca* and *T. marginata*.

Concerning the origin of the tortoises of Sardinia, the analysis of mitochondrial RNA recently suggested that living populations of *T. hermanni* (as well as all the *Testudo* spp.) on Sardinia and other Mediterranean Islands have been introduced by man (Van der Kuyl et al. 2002). Such a conclusion is not supported by the fossil record which shows the presence of *T. hermanni* in the Plio-Pleistocene of Sardinia (Abbazzi et al. 2004) and, above all, in the Middle Pleistocene of Corsica (Hervet & Salotti 2000; Hervet 2001). If a gap in the continuity between these Pleistocene occurrences and the extant populations is present, it is necessary to hypothesize that the introduction operated by man followed (or caused) the extinction of the autochthonous populations on both islands.

Mammalia

Artiodactyla Owen, 1848

Suidae Gray, 1821

Suinae Gray, 1821

Sus Linnaeus, 1758

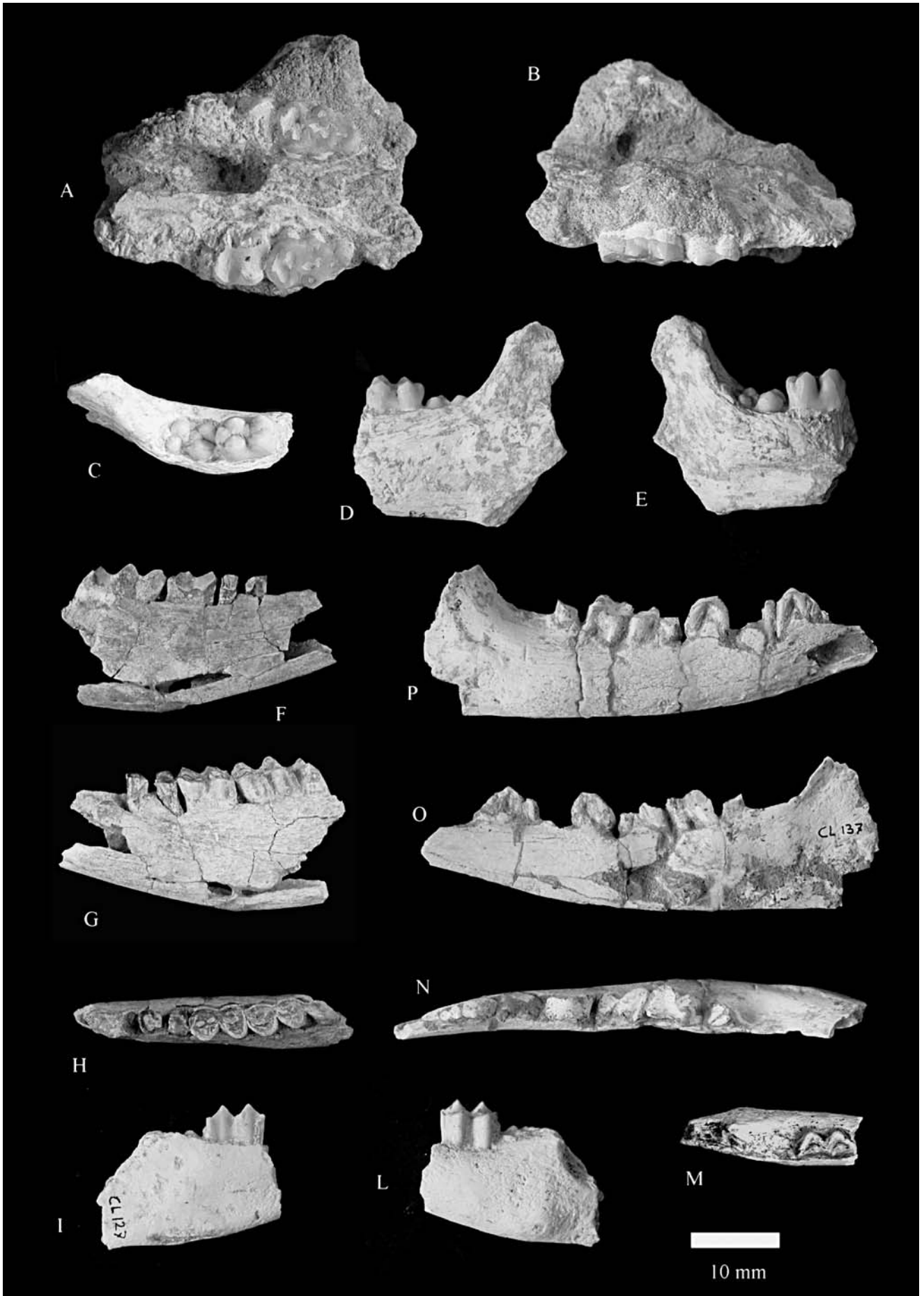
Sus sondaari van der Made, 1999

1980 *Sus scrofa* ssp. Ambrosetti et al., pag. 247.

PLATE 1

Sus sondaari - A, B occlusal and labial views of GP2 incomplete maxillary from the Capo Mannu D4 local fauna, and C, D, E occlusal, lingual and labial views of GP1 fragment of left hemimandible with M₃-M₁ from the Capo Mannu D4 local fauna.

Nesogoral sp. - F, G, H labial, lingual and occlusal views of mandible GP1 from the Capo Mannu D1 local fauna, and I, L, M labial, lingual and occlusal views of CL127 fragment of left hemimandible with M₂ and erupting M₃ from the Capo Mannu D4 local fauna. Small sized bovid of uncertain attribution - N, O, P occlusal, labial and lingual views of CL 137 right hemimandible from Capo Mannu D4 local fauna.



1988 *Sus* aff. *nanus* van der Made - pag. 373, Plate 3, Figs 7-9.
1999 *Sus* aff. *sondaari* van der Made, pag. 347.

Material: Capo Mannu D4 local fauna - GP3, palate; GP4, fragment of mandible; CL123c, right I³; CL106, molar fragment.

Remarks. The palate is poorly preserved and shows only the left M³, a small fragment of the left M², and the right M²-M³ (Plate I, figs. A, B). The M² crown is totally worn. The M³ is also affected by wear, but it is still possible to observe the position of the main cusps and the enamel thickness.

Only the posterior part of the left mandible is preserved (Plate I, figs. C-E). It shows an incompletely erupted M₃ and an M₂. The angle between the horizontal and ascending rami of the mandible seems to be smaller than in recent wild pigs (*Sus scrofa*) but this could be due to diagenetic deformation.

No inferences can be added regarding I³ (crown completely worn) and the small molar fragment.

The dentitions of these new specimens from Capo Mannu D4, although smaller in size (Tab. 1), are similar to the holotype of *Sus sondaari* from Capo Figari (van der Made 1988; 1999) in basic morphology, crown height and enamel thickness.

In the past, three other specimens (a right I², a left I³, and a right P²) from Capo Mannu have been collected in the Capo Mannu D1 interdune by a team of the Instituut voor aardwetenschappen of Utrecht (The Netherlands; IVAU) during the operation of washing sediments in search of micromammals (van der Made, pers. com.). These isolated teeth (kept in the IVAU collections) have been studied by van der Made (1988) and attributed to *Sus* aff. *sondaari*. Van der Made, observing in particular the wear of P², noted that the Capo Mannu suid was a more primitive form because of the unreduced premolar row.

In fact, given the small size of the new Capo Mannu D4 remains, it is likely that the latter had already reduced the premolar row and snout, at least as much as the type population of Capo Figari. The Capo Mannu D4 suid is thus attributed to *Sus sondaari*.

Sus cf. *sondaari* has recently been reported in deposits close to the Plio-Pleistocene transition at Monte Tuttavista (Orosei, Eastern Sardinia, Abbazzi et al. 2004). This material is currently under study.

Sus sondaari from Capo Mannu represents the oldest documentation of the taxon.

Artiodactyla Owen, 1848

Bovidae Gray, 1821

Several fragmentary specimens make the Bovidae the best represented taxon within the large mammal assemblage from the Capo Mannu Fm. Unfortunately

the fragmentary status of most specimens does not allow for a firm taxonomic attribution.

The greater part of the dental remains are referred to the small sized bovid *Nesogoral* sp., this genus being one of the most typical elements of the Sardinian endemic fauna of Pliocene-Early Pleistocene age. A few remains attest to the occurrence of another taxon, significantly larger than *Nesogoral* sp. (Bovidae gen. et sp. indet., see below). Moreover, it is worth underlining that among the fossils of similar size to *Nesogoral* sp., some dentitions do not fully conform to the description of the latter taxon (cf. Gliozzi & Malatesta 1982); therefore, they will be considered separately.

The present study confirms a complex scenario, regarding the dispersal and evolution of Sardinian bovids in the insular environment, which has been already put in evidence by recent investigations. Indeed, the occurrence of a diverse bovid fauna, with more than a single species of *Nesogoral* and with another bovid genus has been reported in the Early Pleistocene fissure infillings at Monte Tuttavista, Orosei (Abbazzi et al. 2004; Palombo et al. 2006). Van der Made (2005) defined the new species *Nesogoral cenisae* from the Middle Pleistocene of Campidano.

Nesogoral sp.

Material: Capo Mannu D1 local fauna - GP1, fragment of left hemimandible with M₃-M₁; GP2, right M¹⁻².

Capo Mannu D4 local fauna - CL127, fragment of left hemimandible with M₂ and erupting M₃; CL138, fragment of right mandible with M₁-D₂; CL123a, left M²; CL120 left M³.

Remarks. The occurrence of *Nesogoral* in the deposits of Capo Mannu (D1 local fauna) was reported by van der Made (1999), who described a few fossils in the IVAU collections, Utrecht. The dentition here considered is characterised by a hypsodont dental crown, the occurrence of the caprine fold, the absence of basal pillars in the lower molars, and mandibles with a horizontal ramus that progressively increases in height from the diastema to a position under M₃ (Plate I, figs. F-M, Tab.1). The features cited above and the size make these

| | M ² DAP | M ² DT | M ³ DAP | M ³ DT |
|-------------|--------------------|-------------------|--------------------|-------------------|
| Capo Mannu | 13.94 | 10.37 | 18.37 | 12.81 |
| Capo Figari | 15.10 | 14.90 | 19.40 | 14.60 |
| | 15.10 | 13.80 | 23.20 | 14.80 |
| | 18.00 | 14.80 | 20.60 | 14.10 |
| | 17.80 | 15.00 | 21.20 | 14.10 |

Tab. 1 - Measurements (mm) of M² and M³ of *Sus sondaari* from Capo Mannu Formation and Capo Figari (holotype). Legend: DAP=maximum length; DT=maximum width.

remains comparable to those referred to the Sardinian endemic bovid *Nesogoral melonii* Dehaut (Gliozzi & Malatesta 1982) which characterises Late Pliocene-Early Pleistocene Sardinian endemic faunas (e.g. “*Nesogoral* complex” according to Sondaar 2000).

The referral of the remains from Capo Mannu to *Nesogoral* sp. is, however, necessary due to the fragmentary state of fossils that hampers detailed comparison.

One of the most peculiar features of *Nesogoral* is the triangular shape of the hemimandibles, found also in the remains from the Capo Mannu formation. This feature, due to the increased height of M₃, occurs as a parallelism among endemic insular bovids, and is seen in *Myotragus* from the Late Miocene-Holocene of the Balearic Islands and in *Maremmia* from the late Miocene Tusco-Sardinian paleobioprovince.

| Specimens | OL | NL | W | H |
|-------------------------------------|------|------|------|------|
| <i>Nesogoral</i> sp. | | | | |
| GP1 M ₃ | 19.5 | 19.1 | 7.8 | 5.7 |
| GP1 M ₂ | 12.8 | 12.7 | 8.4 | 4 |
| GP1 M ₁ | *11 | *11 | - | - |
| CL138 M ₁ | 12.8 | *13 | 6.5 | 6.9 |
| CL127 M ₂ | 13.5 | 12.7 | 7.1 | 6.9 |
| CL123a M ₂ | 16.4 | 15.1 | 14.0 | 8.1 |
| CL120 M ₃ | 15.7 | 14.5 | 14.1 | 5.6 |
| <i>Bovidae</i> undet. (small sized) | | | | |
| CL128 M ₃ | 21.5 | 21.1 | 7.8 | 27.7 |
| <i>Bovidae</i> gen. et sp. indet. | | | | |
| CL129 M ₃ | 24.3 | 24.2 | 9.6 | 20.3 |
| NN M ₂ | 16.2 | * 15 | 10.4 | 16.9 |

Tab. 2 - Measurements (mm) of bovid teeth from Capo Mannu Formation. Legend: OL= occlusal length; NL= length at the neck; W= Width; H= height at the metastylid/mesostyle. * = inferred measurement.

Bovoid remains of small size which do not fully conform to the morphology of *Nesogoral* spp.

Material: Capo Mannu D4 local fauna - CL 137 right hemimandible; Capo Mannu D4 local fauna - CL128, left M₃; CL 105, CL 110, two fragments of lower molars.

Remarks. The morphology of specimen CL 137 (Plate I, Figs N-P) is different in many respects from that of the remains referred to *Nesogoral* sp. from Capo Mannu and from *Nesogoral melonii* found at the type site Capo Figari (Gliozzi & Malatesta 1982). It has a lower and regularly curved horizontal ramus and, on the labial side, lacks the protruding angular tuberosity for the insertion of the masseter muscle, which is present in CL127 and GP1. The completely worn teeth do not allow for further comparisons.

The M₃ (CL128) and the fragmentary lower molars (CL 105, CL 110) are relatively narrower, show less developed stylids, and an almost absent caprine fold (Fig. 7, Tab. 2), compared to *Nesogoral*.

The variability of the above features is poorly known in the fossil samples of *Nesogoral*, which necessitates separate consideration for the remains described in this section.

Bovidae gen. et sp. indet. (larger sized)

Material: Capo Mannu D4 local fauna - CL129, left M₃; CL123b, fragment of upper molar; Not numbered, left M₂.

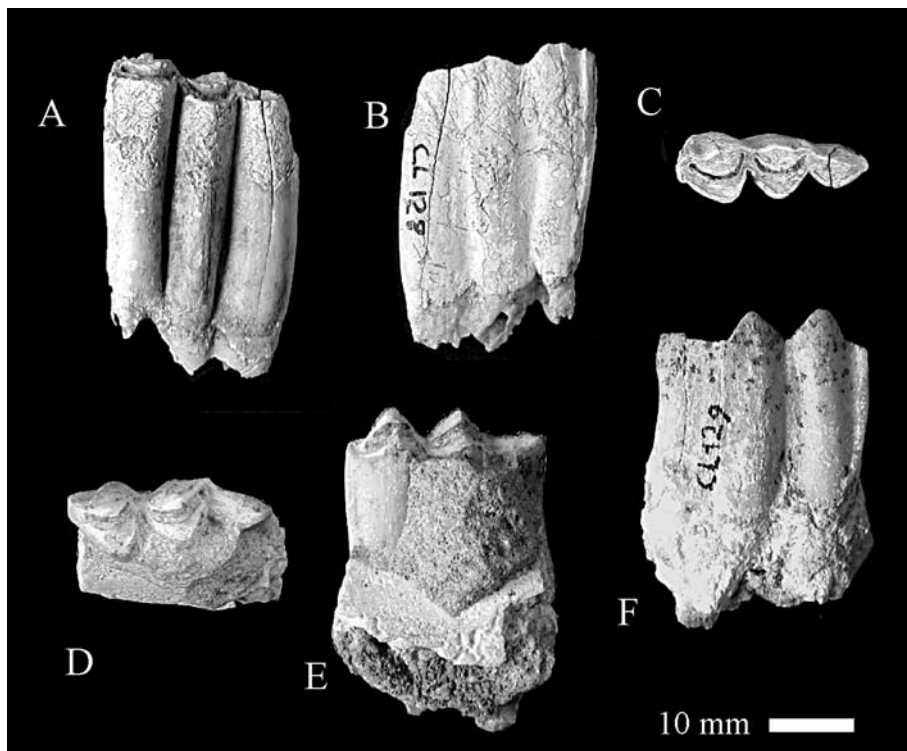


Fig. 7 - Small - sized bovid of uncertain attribution - A, B, C labial, lingual and occlusal views of CL128 left M₃ from Capo Mannu D4 local fauna. *Bovidae* gen. et sp. indet. (large sized) - D, E, F occlusal, labial and lingual views of CL129 left M₃ from Capo Mannu D4 local fauna.

An M_3 and an M_2 are clearly distinct in their larger size (Tab. 2); morphologically, they have more rounded lobes on the lingual side (Fig. 7) compared to the remains referred to *Nesogoral* sp.

Remarks. The bovid postcranial remains from the Capo Mannu D4 local fauna are attributed to two groups on the basis of size differences, without any precise systematic attribution:

Smaller sized remains: CL141a, right metacarpal; CL116, metacarpal; CL112, II phalanx; CL104, unciform; CL118, distal fragment of humerus; CL135, incomplete tibia; CL122, diaphysis of left tibia; CL139, proximal end of left radius; CL133, fragment of diaphysis of radius; CL112, distal fragment of radius; CL 134, and CL136, fragments of pelvis.

Larger sized remains: CL131, incomplete metacarpal; CL 145a and 145b, fragments of metacarpal; CL146, incomplete humerus; CL126, fragment of tuber calcanei; CL126, fragment of diaphysis of metatarsal; CL 108, proximal fragment of metacarpal.

To this undetermined material, can be added a badly crushed fragment of a bovid skull (CL125).

Discussion

The depositional features and the composition of the entire Capo Mannu dune complex suggest particular paleogeographic conditions which are very different from the modern exposed and submerged coastal morphology. The dune accumulation may have resulted from a hot and dry climatic regime with intense aeolian dynamics. The calcareous bioclastic component, as well as the benthic foraminifers are evidence of a transitional continental coastal paleoenvironment during sea-level high stands. Several reddish sediment layers and dune units very rich in terrigenous siliciclastic components are probably related to fluctuations in climate towards cooler and wetter regimes, coinciding with regressive marine eustatic phases. These sediments, likely associated with a climatic-eustatic cyclicality, may be tentatively analysed according to cyclic stratigraphic models to define an upper time limit of the genesis of the entire dune complex. Maximum values on the order of 1 Ma are obtained by correlating the nineteen dune subunits with the astronomical cycles of precession or obliquity of the earth's axis (19-23 or 41-53 ky), and the seven dune units to the cycle of eccentricity of the earth's orbit (97-127 ky), while the minimum values obtained are about 0.4-0.5 Ma. On the basis of such a hypothesis, the deposition of the Capo Mannu Fm. dune complex, starting from the uppermost part of the Mandriola Limestone, would have been completed before the end of the Pliocene.

However, field data show that no clear stratigraphic conformity can be observed between the first dune unit D1 (containing the Capo Mannu D1 local fauna), and the overlying second dune unit D2, because

the contact is covered by Upper Pleistocene MIS 5-2 sediments, while the sequence of dune units from D2 to D7 displays a clear depositional continuity with the presence of the first-order boundaries. The D1 unit directly overlying the Mandriola Limestone is made up of a foraminiferal grainstone, whilst D2 is composed of bioclastic and siliciclastic sands. Together with the different composition of the two units, it can also be observed that D1 shows a higher degree of lithification compared to D2. Therefore, it is not possible to assign a precise age to the end of the accretion of the whole dune complex, or to evaluate the beginning of the erosion phase before the deposition of the Upper Pleistocene MIS 5 beach sediments.

Nevertheless, in the lack of a clear erosional truncation, only an insignificant stratigraphic lacuna, unable to modify substantially the age previously hypothesized on the basis of the cyclic stratigraphic model, could be present between D1 and D2.

As a result, whilst the transition of the shoreface-backshore dune (unit D1) of the Mandriola section can be correlated with the Zanclean-Piacenzian transition, and the overlying D2-D4 units correlate well with the Upper Pliocene, only the thickest of the uppermost dune units of the CFM may have reached the Lower Pleistocene (Fig. 4).

Conclusions

The fossil record of Pliocene vertebrates in Sardinia is relatively poorly known. The Capo Mannu D4 faunal assemblage allows us to partially highlight a chapter of this Pliocene history. Sondaar (2000) introduced the phrase "*Nesogoral* complex" to refer to an assemblage occurring in fissure fillings at Capo Figari (Olbia) and Monte Tuttavista (Orosei) dated to the latest Pliocene-early Pleistocene. The "*Nesogoral* complex" (cf. also Sondaar & Van der Geer 2002) is characterised by the occurrence of endemic species of the murid *Raghapodemus* (*Raghapodemus minor*), the bovid *Nesogoral*, the small suid *Sus sondarii*, and the endemic macaque *Macaca majori*. A recent comprehensive study of the extremely large record from the Monte Tuttavista faunal complexes allowed for the recognition within this "*Nesogoral* complex" of peculiar carnivores like the mustelid *Pannonictis* and the hyaenid *Chasmaporthetes melei*, as well as a differentiated bovid assemblage (Abbazzi et al. 2004; Rook et al. 2003; 2004).

Although the Capo Mannu D4 mammal assemblage does not allow us to derive precise chronological constraints, a few considerations can be made. First of all, the evolutionary stage of the endemic murid *Raghapodemus* from the Capo Mannu D1 local fauna (for-

merly known as “Mandriola”; from an interdune deposit within the basal Capo Mannu Fmt D1 dune unit, cfr. Fig. 2), although already endemized (*Rhagapodemus azzarolii*) shows only incipient modification compared to the later species *Rhagapodemus minor*, typical of the “Nesogoral complex” as defined by Sondaar (2000) and recognized at Monte Tuttavista (Abbazzi et al. 2004).

As a matter of fact, given the biochronologic characterization of *Rhagapodemus azzarolii* (MN 15?; Angelone & Kotsakis 2001) and the above discussed more likely maximum estimate of 1 Ma for the deposition of the entire dune complex — even in case of a minor stratigraphic lacuna between D1 and D2 — the age of the vertebrate remains from the D3-D4 dune units should be constrained within the Late Pliocene, thus

representing the oldest known sample of the “Nesogoral complex”.

Acknowledgments. For profitable discussion and help with comparative collections we are grateful to M. Arca (Nuoro), S. Gentili (Perugia), T. Kotsakis (Rome), M. Palombo (Rome), C. Tuveri (Nuoro), J. van der Made (Madrid), F. de Lapparent de Broin (Paris) kindly offered her assistance for the identification of the tortoise; D. Righi (Modena) discussed the morphology of *T. amiatae*; E. Razzetti (Pavia) suggested relevant literature concerning extant tortoises. We specially thank Dr. Maria Tegas (Lanusei, Sardinia) for the contribution in the discovery of the tortoise during the field survey of her degree thesis.

This paper was presented at the 32nd International Geological Congress, Florence 2004. We thanks M. Chiari (Firenze) for his editorial work on a first version of the manuscript and A. Shabel (Berkeley), M.R. Palombo (Rome) and L. Werdelin (Stockholm) for critical revision of the manuscript.

Research supported by Fondi d’Ateneo grants (LR) and Università degli Studi di Cagliari (M.I.U.R. 60%) grants (SC).

REFERENCES

- Abbazzi L., Angelone C., Arca M., Barisone G., Bedetti C., Delfino M., Kotsakis T., Marcolini F., Palombo M.R., Pavia M., Piras P., Rook L., Torre D., Tuveri C., Valli A.M.F. & Wilkens B. (2004) - Plio-Pleistocene fossil vertebrates of Monte Tuttavista (Orosei, E. Sardinia, Italy), an overview. *Riv. It. Paleont. Strat.*, 110(3): 603-628, Milano
- Ambrosetti P., Azzaroli A. & Kotsakis T. (1980) - Mammi-feri del Plio-Pleistocene delle isole. In: I Vertebrati fossili italiani: 243-348, Museo Civico di Storia Naturale di Verona, Verona
- Amiranashvili N.G. (2000) - Differences in shell morphology of *Testudo graeca* and *Testudo hermanni*, based on material from Bulgaria. *Amphibia-Reptilia*, 21: 67-81, Leiden.
- Amori G., Angelici F.M., Frugis S., Gandolfi G., Groppali R., Lanza B., Relini G. & Vicini G. (1993) - Vertebrata. In: Minelli A., Ruffo S. & La Posta S. (Eds) - Checklist delle specie della fauna d’Italia. Vol. 110, IV + 83 pp., Calderini, Bologna.
- Angelone C. & Kotsakis T. (2001) - *Rhagapodemus azzarolii* n. sp. (Muride, Rodentia) from the Pliocene of Mandriola (Western Sardinia - Italy). *Boll. Soc. Paleont. Ital.*, 40(2): 127-132, Modena.
- Batsch G.C. (1788) - Versuch einer Unleitung, zur Kenntnis und Geschichte der Thiere un Mineralien. *Jena, Ackad. Buchh.*, 1: i-vi, 1-528, Iena.
- Beccaluva L., Civetta L., Macciotta G. & Ricci C.A. (1985) - Geochronology in Sardinia: results and problems. *Rend. Soc. Ital. Mineral. Petrogr.*: 40, 57-72, Varese.
- Brongniart A. (1800) - Essay d’une classification naturelle des Reptiles. *Bull. Soc. philomat.*, 3, 2, 11 (=35): 81-82; 12 (=36): 88-91, Paris.
- Brookfield M.E. (1977) - The origin of bounding surfaces in ancient aeolian sandstones. *Sedimentology*, 24: 303-322, Oxford.
- Carboni S. & Lecca L. (1985) - Osservazioni sul Pleistocene Medio-Superiore della penisola del Sinis (Sardegna occidentale). *Boll. Soc. Geol. Ital.*, 104: 459-477, Roma.
- Carboni S. & Lecca L. (1995) - Le Pliocène de Capo Mannu (Sardaigne occidentale): transition marin littoral-continental dunaire. *C.R. Acad. Sci. Paris*, 320, sér. II a: 1203-1210, Paris.
- Cherchi A., Marini A., Murru M. & Robba E. (1978) - Stratigrafia e paleoecologia del Miocene superiore della Penisola del Sinis (Sardegna occidentale). *Riv. It. Paleont. Strat.*, 84(4): 973-1036, Milano.
- Delfino M. (2002) - Erpetofaune Italiane del Neogene e del Quaternario. Doctoral Dissertation Thesis. 382 pp., Modena and Reggio Emilia University.
- Esu D. (1984) - La malacofauna continentale pliocenica di Mandriola (Sardegna occidentale): sistematica e paleobiogeografia. *Geologica Romana*, 23: 23-50, Roma.
- Esu D. & Kotsakis T. (1979) - Restes de Vertébrés et de Mollusques continentaux dans le Villafranchien de la Sardaigne. *Géobios*, 12(1): 101-106, Lyon.
- Esu D. & Kotsakis T. (1983) - Les vertébrés et les mollusques continentaux du Tertiaire de la Sardaigne: paléobiogéographie et biostratigraphie. *Geologica Romana*, 22, 177-206, Roma.
- Francolini L., Lecca L. & Mazzei R. (1990) - La presenza del Pliocene inferiore nella piattaforma continentale della Sardegna occidentale. *Atti Soc. Tosc. Sci. Nat.*, Mem., Ser. A, 97: 93-111, Pisa.
- Gliozzi E. & Malatesta A. (1982) - The Quaternary Goat of Capo Figari (Northeastern Sardinia). *Geologica Romana*, 19 (1980); 295-347, Roma.
- Gray J.E. (1821) - On the natural arrangement of vertebrate animals. *London Medical Repository*, 15; 296-310, London.
- Guyot Jackson G. (ed.) (2004) - Numéro spécial - *Testudo Manouria*, 7(22): 1-52, Mezzavia.

- Hervet S. (2001) - Étude du peuplement chelonien de la Corse à partir de la repartition des tortues fossiles de la Méditerranée occidentale. *Bull. Soc. Sci. Hist. Nat. Corse*, 696-697: 147-163, Bastia.
- Hervet S. & Salotti M. (2000) - Pleistocene turtles from Castiglione (Oletta, Corsica) and evidence of indigenous population in Corsica. *C.R. Acad. Sci. Paris*, ser. II a, 330(9): 645-651, Paris.
- Kotsakis T. (1980) - Osservazioni sui Vertebrati quaternari della Sardegna. *Boll. Soc. Geol. Ital.*, 99: 151-165, Roma.
- Lanza B. & Corti C. (1993) - Erpetofauna italiana: "acquisizioni" ed estinzioni nel corso del novecento. *Supp. Ric. Biol. Selvaggina*, 21: 5-49, Bologna.
- Lapparent de Broin de F. (2000) - African chelonians from the Jurassic to the present: phases of development and preliminary catalogue of the fossil record. *Palaeont. afr.*, 36: 43-82, Johannesburg.
- Lapparent de Broin de F. (2001) - The European turtle fauna from the Triassic to the Present. *Dumerilia*, 4: 155-217, Paris.
- Lapparent de Broin de F. (2002) - A giant tortoise from the Late Pliocene of Lesbos Island (Greece) and its possible relationships. *Ann. Géol. Pays Helléniques*, 39(A): 99-130, Athens.
- Lecca L. & Carboni S. (2007) - The Tyrrhenian section of San Giovanni di Sinis (Sardinia): stratigraphic record of an irregular single high stand. *Riv. It. Paleont. Strat.*, 113(3): 509-523, Milano.
- Lecca L., Carboni S., Scarteddu R., Pisano S., Sechi F. & Tilocca G. (1986) - Schema stratigrafico della piattaforma continentale occidentale e meridionale della Sardegna. *Mem. Soc. Geol. It.*, 36: 31-40, Roma.
- Linnaeus C. (1758) - Systema Naturae. Ed. 10, Vol. I, Regnum Animale. Holmiae (Stockholm), L. Salvii, 1-824, Stockholm.
- Owen R. (1848) - Contributions to the History of British Fossil Mammals. 71 pp., Taylor, London.
- Palombo M.R., Valli A.M.F., Arca M. & Tuveri C. (2006) - A new bovid, *Asoletragus gentryi* n. gen. et sp., from Monte Tuttavista (Orosei, Eastern Sardinia, Italy). *Riv. It. Paleont. Strat.*, 112(3): 459-471, Milano.
- Pecorini G., Rage J.-C. & Thaler L. (1974) - La Formation continentale de Capo Mannu, sa faune de Vertébrés pliocènes et la question du Messinien en Sardaigne. *Rend. Sem. Fac. Sc. Univ. Cagliari*, suppl. vol. 43: 305-320, Bologna.
- Rook L., Abbazzi L., Angelone C., Arca M., Barisone G., Bedetti C., Delfino M., Kotsakis T., Marcolini F., Palombo M.R., Pavia M., Piras P., Torre D., Tuveri C., Valli A. & Wilkens B. (2003) - Osservazioni preliminari sui vertebrati fossili Plio-Pleistocenici del Monte Tuttavista (Orosei, Sardegna). *Sardinia Corsica et Baleares Antiquae*, 1: 11-29, Pisa-Roma.
- Rook L., Ferretti M.P., Arca M. & Tuveri C. (2004) - *Chasmaporthetes melei* n. sp., an endemic Hyaenid (Carnivora, Mammalia) from the Monte Tuttavista fissure fillings (Late Pliocene to Early Pleistocene; Sardinia, Italy). *Riv. It. Paleont. Strat.*, 110(3): 639-646, Milano.
- Sondaar P.Y. (2000) - Early Human Exploration and Exploitation on Islands. *Tropics*, 10: 203-230, Kagoshima.
- Sondaar P.Y. & Van der Geer A. (2002) - Plio-Pleistocene vertebrate faunal evolution on Mediterranean islands, compared to that of the Palearctic mainland. *Ann. Géol. Pays Helléniques*, 39(A), 165-180, Athens.
- Tegas M. (2000) - Contributo alla stratigrafia del Pliocene, Pleistocene ed Olocene del Sinis nord-occidentale. Unpublished Thesis, Università degli Studi di Cagliari, 144 pp.
- Van der Kuyl A.C., Ballasina D.L.P., Dekker J.T., Maas J., Willemsen R.E. & Goudsmit J. (2002) - Phylogenetic relationships among the species of the genus *Testudo* (Testudines: Testudinidae) inferred from mitochondrial 12S rRNA gene sequences. *Mol. Phylog. Evol.*, 22: 174-183, Amsterdam.
- Van der Made J. (1988) - *Sus nanus* nov. sp., a Pliocene dwarf pig from Capo Figari (Northeastern Sardinia). *Boll. Soc. Paleont. Ital.*, 27(3): 367-378, Modena.
- Van der Made J. (1999) - Biogeography and stratigraphy of the Mio-Pleistocene mammals of Sardinia and the description of some fossils. In: Reumer J.W.F. & De Vos J. (Eds) - "Elephants have a snorkel! Papers in honour of Paul Y. Sondaar", *Deinsea*, 7: 337-360, Rotterdam.
- Van der Made J. (2005) - The fossil endemic goat *Nesogoral cenisae* n. sp. from Campidano, Sardinia - Cursorial adaptations in insular environment. In: Alcover J.A. & Bover P. (Eds) - "Insular Vertebrate Evolution: the Palaeontological Approach", *Monografies de la Societat d'Historia Natural de les Balears*, 12: 347-368, Palma de Mallorca.